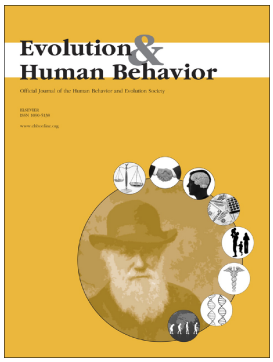
Smith, D., Dyble, M., Major, K., Page, A. E., Chaudhary, N., Salali, G. D., Thompson, J., Vinicius, L., Migliano, A. B., & Mace, R. (2019). A friend in need is a friend indeed: Need-based sharing, rather than cooperative assortment, predicts experimental resource transfers among Agta hunter-gatherers. *Evolution and Human Behavior*, *40*(1), 82-89. https://doi.org/10.1016/j.evolhumbehav.2018.08.004



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PII: S1090-5138(18)30123-5
DOI: doi:10.1016/j.evolhumbehav.2018.08.004
Reference: ENS 6232

To appear in: *Evolution and Human Behavior*

Received date: 7 May 2018
Revised date: 13 August 2018
Accepted date: 13 August 2018

Please cite this article as: Daniel Smith, Mark Dyble, Katie Major, Abigail E. Page, Nikhil Chaudhary, Gul Deniz Salali, James Thompson, Lucio Vinicius, Andrea Bamberg Migliano, Ruth Mace , A Friend in need is a Friend indeed: Need-based sharing, rather than Cooperative Assortment, Predicts Experimental Resource Transfers among Agta Hunter-Gatherers. Ens (2018), doi:10.1016/j.evolhumbehav.2018.08.004

A Friend in Need is a Friend Indeed: Need-Based Sharing, Rather than Cooperative Assortment, Predicts Experimental Resource Transfers among Agta Hunter-Gatherers

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Word count: 6,577 (excluding references)

Abstract

Despite much theorizing, the evolutionary reasons why humans cooperate extensively with unrelated individuals are still largely unknown. While reciprocity explains many instances of non-kin cooperation, much remains to be understood. A recent suite of models based upon 'cooperative assortativity' suggest that non-kin cooperation can evolve if individuals preferentially assort with certain cooperative phenotypes, such as helping those who help others. Here, we test these assortative hypotheses among the Agta, a population of Filipino hunter-gatherers, using an experimental resource allocation game in which individuals divide resources between themselves and camp-mates. Individuals preferentially shared with less cooperative individuals, arguing against cooperative assortativity as a mechanism sustaining resource transfers in this population. Rather, sharing was often based on the recipient's level of need, in addition to kin-based transfers and reciprocal sharing. Contrary to several recent theoretical accounts, in this real-world setting we find no evidence for cooperative assortativity influencing patterns of cooperation. These results may reflect the demands of living in a foraging ecology characterized by high resource stochasticity, necessitating need-based sharing as a system of long-term reciprocity to mitigate repeated subsistence shortfalls.

Keywords: Cooperation; Assortativity; Need-Based Sharing; Reciprocity; Hunter-Gatherers; Experimental Games.

1. Introduction

The question of why organisms display cooperative behavior – defined as a behavior which evolved to benefit others (West, Griffin, & Gardner, 2007b) – has been central to biology for over 50 years (Hamilton, 1964; Nowak, 2006). Although kin selection, where cooperation between relatives provides indirect fitness benefits (Hamilton, 1964), and reciprocity, where repeated cooperative interactions lead to greater long-term pay-offs than short-term defection (Trivers, 1971), explain many instances of cooperation throughout the animal kingdom (West, Griffin, & Gardner, 2007a), they appear insufficient to explain the full range of observed cooperative behavior. This is especially true in humans where cooperation is often between unrelated individuals who, particularly in modern market-based economies, may not interact again in the future (Nowak & Sigmund, 2005).

One potential theory to explain the human propensity for cooperation is indirect reciprocity, which suggests that organisms may help others if this increases their reputation as a cooperative individual, resulting in greater cooperation from others in the future (Alexander, 1987; Nowak & Sigmund, 1998, 2005; Panchanathan & Boyd, 2003). Crucially, the evolution of indirect reciprocity depends upon preferential cooperation towards these cooperative individuals ('helping those who help others'). Theories such as competitive altruism (also known as 'reputation-based partner choice') make similar predictions, such that cooperative individuals should be preferentially cooperated with (Roberts, 1998; Sylwester & Roberts, 2013). However, the mechanisms are distinct; competitive altruism is based on the principle of signaling cooperativeness to form future mutually-beneficial cooperative ventures, while indirect reciprocity does not require future repeated interactions. Nonetheless,

both accounts are theories of 'cooperative assortativity', which suggest that cooperation can evolve if individuals preferentially cooperate with cooperative others.

In support of these theories, several lab studies have shown that cooperative individuals receive more help from others, even if they have never previously interacted (Milinski, 2016; Raihani & Barclay, 2016; Sylwester & Roberts, 2013). However, whether these patterns extend to real-world interactions where multiple forms of information can also be used on which to base cooperation, such as kinship or previous interactions, is largely an open question. Field studies have shown that individuals respond to threats to their reputation with increased cooperation (Yoeli, Hoffman, Rand, & Nowak, 2013), while sellers on eBay with a good reputation are more likely to attract customers (Livingston, 2005). However, whether people selectively cooperate with more cooperative individuals remains under-explored in real-world settings. Small-scale populations, where group sizes are small and acts of cooperation frequent – including food-sharing (Gurven, 2004), childcare (Hrdy, 2009), cooperative foraging (Hill, 2002), labor-sharing (Jaeggi, Hooper, Beheim, Kaplan, & Gurven, 2016) and political coalitions (Patton, 2005) – are particularly useful to explore how factors such as cooperativeness, kinship, reciprocity, and other considerations, influence cooperative decision-making. Research in small-scale societies, particularly hunter-gatherers, may also provide insights regarding the social and ecological bases of human cooperative evolution prior to the development of agriculture and large-scale societies (Lee & Daly, 1999).

In several foraging populations the most cooperative individuals, such as those who share the most food, do not necessarily receive more in return (Bliege Bird, Bird, Smith, & Kushnick, 2002; Kaplan & Hill, 1985). Among the Hadza, using a Public Goods Game to measure cooperation, the most cooperative individuals were

not more likely to be given resources or nominated as social partners (Apicella, Marlowe, Fowler, & Christakis, 2012). However, among Dominican bay oil producers, individuals with a reputation for cooperativeness were preferred recipients of cooperation (Macfarlan, Remiker, & Quinlan, 2012), while Hiwi who invested more time in foraging received more resources than others (Gurven, 2006). Although this pattern was not found among Ache foragers (Gurven, 2006), Ache who consistently provisioned others were more likely to receive resources when they were sick or injured (Gurven, Allen-Arave, Hill, & Hurtado, 2000). In summary, there is only partial support for models of cooperative assortativity in small-scale societies.

A related theory also based on assortativity posits that cooperation can evolve if agents assort according to cooperative homophily; that is, cooperating with others of a similar cooperative level (Apicella et al., 2012). However, it is unclear why, in the absence of other mechanisms, non-cooperators would preferentially assort with other non-cooperators. While cooperative homophily is an *outcome* of the above processes based on cooperative assortment, via mechanisms such as 'walk away' or partner choice (Aktipis, 2004; Lewis, Vinicius, Strods, Mace, & Migliano, 2014; McNamara, Barta, Fromhage, & Houston, 2008), these mechanisms do not require that defectors actively seek out other defectors. Nonetheless, Hadza individuals were more likely to nominate to live and cooperate with others of a similar cooperative level to themselves, suggesting that assortativity by cooperative homophily may occur and is not merely an outcome of other assortative processes (Apicella et al., 2012). There are therefore two pathways by which cooperative assortment may facilitate the evolution of cooperation: cooperating with the most cooperative individuals (indirect reciprocity and competitive altruism) and cooperating with others of a similar cooperative level (cooperative homophily).

As discussed above, contrary to expectations based on cooperative assortativity in several populations the most cooperative individuals are not preferred cooperative partners. This behavior may reflect need-based sharing, where those in greater need receive more assistance (Aktipis, Cronk, & de Aguiar, 2011). In studies of forager food-sharing, those with a larger family or with low calorific production relative to family consumption, and therefore in greater need, tend to receive more resources (Allen-Arave, Gurven, & Hill, 2008; Gurven, Hill, Kaplan, Hurtado, & Lyles, 2000), while Agta foragers were more likely to receive resources from others if they were unable to procure resources on a given day (Dyble et al., 2016). Consistent with this, Agta in less need were more cooperative in an experimental game (Smith et al., 2016), while lower socioeconomic status has been associated with reduced cooperation in developed countries (Silva & Mace, 2014). Similarly, in an experimental game among Fijians, the most common reason for sharing was the relative need of the recipient (Gervais, 2017).

However, in the absence of other mechanisms need-based sharing is a description of cooperation, not an adaptive evolutionary explanation; a strategy of altruistic donations to those in need, without any subsequent future fitness gain, is unlikely to be selected for. This situation is comparable to the 'Banker's Paradox' (Tooby & Cosmides, 1996), where the individuals most in need of a loan (or resources) are the least likely to receive them because they are a greater 'credit risk' and less likely to repay the loan. Nonetheless, these observed need-based transfers may be adaptive if they reflect direct reciprocity, where individuals with resources help those in need – as the costs to giving are low and the benefits to the recipient are high – which may be reciprocated in the future (Trivers, 1971). Although research on forager food-sharing has indicated the presence of need-based

transfers (Allen-Arave et al., 2008; Gurven, 2004; Hooper, Gurven, Winking, Kaplan, & Hooper, 2015), from these observational studies it is difficult to assess whether these patterns are a result of giving to those in need (i.e., cooperation) or needy individuals taking resources from those with more resources, as predicted by models of tolerated theft (Blurton Jones, 1987; Winterhalder, 1996). Experimental studies which dissociate unsolicited giving from tolerated theft can be used to help answer these questions.

Here we explore resource transfers among Agta hunter-gatherers to test predictions of indirect reciprocity/competitive altruism and cooperative homophily. We use a novel experimental game in which resources are divided between self and known camp-mates. Using this approach, we previously found that individuals preferentially shared resources with both kin and reciprocal partners (Smith et al., 2016). We now extend this analysis to explore how an individual's cooperativeness influences their probability of receiving resources from others. Specifically, we test whether the Agta: i) preferentially share resources with cooperative individuals (in line with theories of indirect reciprocity and competitive altruism); and ii) share resources with others of a similar cooperative level (as predicted by cooperative homophily).

2. Methods

2.1. Ethnographic Background

This study focuses on two Agta sub-populations, the Palanan Agta (~1,000 individuals) and the Maconacon Agta (~250 individuals) from the remote Northern Sierra Madre Natural Park in northeast Luzon, the Philippines. They subsist predominantly as hunter-gatherers, engaging in hunting, fishing and gathering of wild

resources, but also in wage or agricultural labor when available. Of the time spent in economic activities, 77% concerned foraging behavior, predominantly fishing (54%), but also gathering (20%) and hunting (3%), while the remaining 23% of time was spent engaged in non-foraging behavior, such as cultivation (13.5%) and wage labor (9.5%; Page et al., 2016). Game and fish are traded with local agricultural non-Agta populations for rice, other carbohydrates and luxury goods. Food-sharing is a regular daily occurrence (Dyble et al., 2016). Camp sizes vary between solitary dwellings (seven individuals) to large camps with 26 houses (156 individuals), with an average of seven houses (49 individuals).

2.2. Data Collection

An experimental resource allocation game – the 'Sharing Game' (SG) – was played with 290 Agta (mean age=37, range=16-70, males=140) from 18 camps (324 Agta were included as potential recipients, but 34 Agta did not play the game due to either moving camp or subsequently deciding not to take part). Participants were shown their own picture, along with a maximum of 10 other randomly-selected adults from camp (individuals from camps with ≤10 other camp-mates were shown all other adults) and given a number of small wooden tokens (each representing 125g of rice; approximately a meal for one individual) equal to the number of camp-mate photos (i.e., in a camp of 11 individuals (10 camp-mates plus ego) each player would be given 10 tokens, while in a camp of nine individuals (eight camp-mates plus ego) each player would be given eight tokens). This was chosen so that not all pictures, including ego, could receive rice. For each token, participants had to decide whether to keep the rice (placing the token on their own picture) or give it to a camp-mate of their choosing (placing the token on the camp-mate's picture). For each resource given, participants were asked why that recipient was selected. This was repeated

until no tokens remained. Prior to leaving camp, the amount of rice earned by each participant was given to them (the amount they kept for themselves plus the amount they received from others).

Decisions were made in private, with just the experimenter, translator and participant aware of an individual's decisions. Other camp-mates were not made aware of any other player's decisions. The experimenter read the game instructions in English, which were then translated into the participant's local language (Tagalog, Paranan or Ilocano). All field assistants were trained prior to fieldwork to ensure that they understood the game rationale and procedures. Approximately ten days were spent at each Agta camp. Upon entering the camp, Agta were informed that experimental sharing games would be played with all consenting adult members of the camp. Games were conducted on the last few days in order to maximize familiarity with the researchers and facilitate trust, but also to minimize the potential for collusion between camp-mates. We do not believe that this occurred, as there were no sudden shifts in game behavior over time.

This non-anonymous game structure was used to assess both levels of cooperative behavior and patterns of cooperation (i.e. who individuals share with, such as kin or those who shared reciprocally). The game is similar to the 'Gift Game' conducted in several populations (Apicella et al., 2012; Chaudhary et al., 2015; He, Wu, Ji, Tao, & Mace, 2016; Thomas, Næss, Bårdsen, & Mace, 2015) where participants are given resources (e.g. sticks of honey) and have to decide who to give it to. Although the game used here is structurally alike, it possesses the added rule that participants could either keep a share for themselves if they wished or give it to a camp-mate of their choosing. Although the Gift Game allows the choice of giving to multiple individuals, it does not measure levels of cooperation as there is no

option for keeping gifts for one's self, meaning that there is no conflict between individual and group interests. On the other hand, although traditional economic games, such as the Ultimatum Game, Dictator Game, and Public Goods Game, measure levels of cooperation, they include only anonymous partners, and therefore ignore the role that differences in relationship have on cooperation (Rucas, Gurven, Kaplan, & Winking, 2010) and cannot be used to explore who individuals preferentially share resources with.

After preliminary trials with different resources, it was decided that rice would be used as the game resource as it is highly sought-after by the Agta and therefore carries enough value to cause a dilemma when deciding whether to share or not. Initial trials with other goods, such as honey sticks, were perceived to have little value (and were freely distributed to children). After discussing with the Agta which resources were most valued, rice was the unanimous choice. The Agta do not grow their own rice (although they may harvest it for neighboring agricultural populations), and although it is a non-foraged commodity introduced by non-Agta agricultural populations it is one of the Agta's primary sources of calories (when available) and is highly valued.

2.3. Statistical Analyses

The response variable was coded in a matrix as '1' if ego (the giver) gave to alter (the recipient) and '0' if not (note that although givers could theoretically donate more than one gift to a single recipient, in practice only one individual gave two tokens to the same individual, hence the use of a binary term here). Between-camp dyads and camp-mates not presented to ego were coded as missing. The main independent variable of interest was 'alter cooperation score', reflecting the recipient's level of cooperativeness. Each individual possessed a score (between 0%

and 100%) indicating the percent of gifts donated to others, with 0% meaning no resources shared with camp-mates (all gifts kept for self) and 100% meaning all resources shared with camp-mates (no gifts kept for self). For each individual this was centered around the mean for each camp (camp mean minus individual score), so that between-camp differences in cooperation did not confound within-camp sharing patterns. Individuals with a positive score gave more than others in camp (i.e., they were more cooperative than the camp average). 'Cooperative homophily' was also included as a predictor variable to explore whether individuals gave to others of a similar cooperative level. This was constructed by assessing the difference in cooperativeness between ego and alter. For instance, a difference of '0' meant that both individuals gave the same, while '30' indicated a difference, irrespective of direction, of 30 percentage points between ego and alter. As reported previously (Smith et al., 2016), the average amount of rice kept in the Sharing Game was 62.6% (SD=30.5), which varied considerably between camps, with individuals from the most cooperative camp keeping on average only 26.8% of rice for themselves, while in the least cooperative camp no camp-mates shared any resources (figure 1 in *ibid*.).

Following similar methodologies in other hunter-gatherer populations (Apicella et al., 2012), we make the assumptions that: i) individuals know who the most cooperative people are; and ii) that this is reflected in how much individuals share in the game. Given that the Agta have known their camp-mates for most of their lives we believe that the first assumption is plausible. Decisions about an individual's trustworthiness are made within a fraction of a second (Willis & Todorov, 2006), while strangers could predict who would cooperate after interacting for only 30 minutes (Frank, Gilovich, & Regan, 1993). Multiple years of exposure are likely to

result in more accurate judgments regarding cooperativeness among the Agta. Secondly, although traditional economic games, such as the Ultimatum, Dictator or Public Good Games, often have questionable external validity (Gurven & Winking, 2008; Winking & Mizer, 2013; although see Peysakhovich, Nowak, & Rand, 2014), we have previously demonstrated that these contextualized non-anonymous games among the Agta mirror real-world food-sharing decisions (Smith et al., 2016; see also Gervais, 2017). Individuals from camps who shared food reciprocally in the real-world were both more likely to share resources in these games and to share these experimental resources reciprocally, consistent with the idea that reciprocal sharing requires producer control with individuals willing to share resources with others (Smith et al., 2016). This suggests that the Agta's levels of cooperativeness in this game likely reflect cooperativeness in the real-world, at least regarding food-sharing decisions, providing some confidence that the second assumption is also valid.

Additional variables included: kinship relation between ego and alter, reciprocity, proximity, age (of ego, alter, and age difference) and sex (of ego, alter, and whether same or different sex). Kinship relations were defined as: primary kin (PK), with a relatedness coefficient of r=0.5 to ego; distant kin (DK), with a relatedness coefficient between r=0.03125 (second cousins) and r=0.25 to ego; spouse; spouse's primary kin/primary kin's spouse (SPK/PKS); spouse's distant kin/other affines (SDK/OA), which includes distant kin of spouse or other affinal relationships up to five steps away from ego (e.g., spouse's brother's wife's mother); and non-relatives (NR), which includes everyone else without a kinship link to ego (see Dyble et al., 2015 for further details). Each of these categories was compared relative to resources given to non-kin. The matrix for reciprocity was the transpose of the response variable (i.e., whether alter gave to ego), from which it is possible to

assess whether individuals were more likely to share with camp-mates who also shared with them. Although decisions in this game were made without knowing how others behaved, we justify this definition of 'reciprocity' by noting that reciprocity requires individuals sharing with camp-mates who they expect to share back in return, which can be assessed using this experimental design. Proximity was coded from one to four, reflecting increasing physical distance between ego and alter, with categories of: living in the same house as ego (1); living in the house next to ego (2); having a house between ego's and alter's (3); and living further away (4).

In order to ensure that patterns of resource transfers were not confounded by the amount an individual distributed, ego's cooperative score (% donated to others) was included as a control variable in all models. As a consequence of the game structure, reciprocity could not be measured for all individuals in larger camps, resulting in 1,312 dyads (out of a total 2,752) containing the reciprocity variable. Similarly, as not all 324 potential recipients played the game, alter cooperativeness and cooperative homophily scores were only available for 2,530 dyads. Of these 1,312 dyads, the number of potential recipients in each kinship category is displayed in table S1. Note also that even though 290 Agta participated in these games, these analyses include only the 272 individuals with at least one potential reciprocal partner.

Analyses were conducted using the statistical software *R* 3.5.0 (R Development Core Team, 2018). A generalized estimation equation (GEE) approach was utilized to control for repeated data from the same individual (Zeger & Liang, 1986). Logistic regressions exploring whether ego gave to alter were conducted on vectors containing the variables described above. Due to GEE analyses not utilizing full-likelihood estimates, quasi-likelihood information criterion estimates (QIC; Pan,

2001) were employed to compare model fit. A global model was constructed first containing all variables described above. Keeping ego cooperative score, age and sex constant in all models as control variables, all possible combinations of models containing the theoretically-relevant variables (kinship, reciprocity, proximity, alter cooperativeness, and cooperative homophily) were constructed and QIC values compared. Models within two QIC values of the top model were subsequently put forward for model averaging to account for model uncertainty and identify the factors most strongly associated with receiving resources (see 'Supplementary Information' for further details of this model comparison approach). All models contained the same 1,312 dyads to ensure that QIC values were comparable between models.

Continuous input variables were standardized over two standard deviations (SDs; Gelman, 2008). This standardization allows direct comparison of effect sizes between both continuous and binary variables, as well as between continuous variables on different scales. Unless otherwise stated, standardized estimates are used in text, while standardized and unstandardized estimates are displayed in tables (although only unstandardized coefficients are biologically meaningful; Schielzeth, 2010). To facilitate comprehension of effect sizes, log-odd coefficients are converted to odds ratios (OR) in text. Odds ratios for binary or categorical variables are compared to the reference, while odds ratios for continuous variables reflect a 2 SD difference.

3. Results

Out of 1,312 potential recipients, 492 received resources (37.5%). Of the 32 candidate models, those within two QIC values of the top model are displayed in table 1. After model averaging, kinship, reciprocity and alter cooperativeness were each associated with sharing resources (figure 1; see also table S2 for log-odds

estimates and confidence intervals). Consistent with a previous publication (Smith et al., 2016), primary kin (OR=4.01) and distant kin (OR=1.78) were more likely to receive resources than non-kin, while individuals also displayed reciprocity, as they were more likely to nominate others who also gave to them (OR=1.68).

A strong effect of alter cooperative score was reported, with individuals increasingly likely to give to less cooperative individuals (figure 1). A 2 SD decrease in alter cooperativeness was associated with an approximately 50% increase in the likelihood of alter receiving resources (OR=1.58). No effects of cooperative homophily or proximity were found. Other predictive effects included alter age, with a 2 SD increase in recipient age raising the probability of being given to by nearly 50% (OR=1.49), and sex-similarity, with individuals of the same sex nearly twice as likely to receive resources relative to opposite sex dyads (OR=1.89).

In order to explore whether this effect of sharing with less cooperative camp-mates varied by relatedness we compared the baseline global model (containing all variables) to a model containing an interaction term between alter cooperativeness and kinship. Compared to the global model, inclusion of an alter cooperativeness by kinship interaction term resulted in a reduced model fit (global model QIC=1090.3; interaction model QIC=1097), indicating that the effect of giving to less cooperative individuals was approximately equivalent across all kinship categories.

Although GEE models control for repeated observations of givers, they do not control for repeated observations of recipients, which has the potential to bias parameter estimates due to the structural non-independence of the data. Therefore, to test the robustness of these results logistic mixed-effect models with both givers and receivers as random effects were constructed and an identical model averaging approach performed. This model is qualitatively identical to that of the GEE model,

demonstrating the validity and robustness of these results (Table S3). Additionally, in a simplified model containing just ego cooperative score as a fixed effect, along with givers and receivers as random effects, the inclusion of camp as an additional random effect did not improve model fit (camp-level random effect model AIC=1125.8; model without camp-level random effect AIC=1123.8). This indicates that any residual clustering of cooperative decision-making based on camp membership is minimal and unlikely to bias parameter estimates, further highlighting the robustness of the above findings.

3.1. Effect of Need on Resource Transfers

As discussed in the introduction, in several small-scale societies sharing with less cooperative individuals (e.g., those who share less food than others) may indicate need-based sharing. To directly explore the effect of need on resource transfers, additional models were constructed using a composite 'recipient need' variable, based on data from outside the game context. This was based on: i) number of dependent offspring (those aged 15 or younger, as assessed from genealogical interviews), as the amount of resources necessary to support a family increases with the number of non-producing consumers in a household (Hill & Hurtado, 2009); ii) resource availability (whether the household had any rice stored, as assessed from household questionnaires), and iii) an age component, with all individuals under 40 years of age treated as equally needy, followed by a monotonic increase in need after this age. This age component was chosen because foraging returns among hunter-gatherers tend to decline after this age (Dyble et al., 2016; Hill & Hurtado, 2009), rates of morbidity and mortality increase (Kaplan, Hill, Lancaster, & Hurtado, 2000) and individuals become weaker and more dependent on others (Draper & Harpending, 1994), all of which are indicative of being in greater need.

Comparable measures of need have been utilized in other studies exploring food-sharing and cooperation more generally (e.g., Gurven, Hill, et al., 2000; Hames & McCabe, 2007; Thomas et al., 2018).

Continuous variables of family size and age were standardized over 2 SDs to make them comparable with the binary resource availability variable (which was standardized around its mean; Gelman, 2008). The average of these three standardized variables was then taken to estimate an individual's level of need, with a greater value indicating greater need. To demonstrate the validity of this composite need variable, a linear regression controlling for sex found that individuals in need were lighter than less-needy individuals, with a one unit increase in need predicting a 2.75 kilogram decrease in weight (95% CI: [-0.43; -5.06], p=0.02, n=276). Alter age was also removed from subsequent analyses to avoid confounding with need, as the two are highly correlated (r=0.66, p<0.001, n=324).

Compared to a baseline model containing all predictor variables other than need, the model with alter need possessed a superior model fit, over two QIC values lower than the baseline (baseline model QIC=1093.3; need model QIC=1089.6). This model found that individuals in greater need were more likely to receive resources (b=0.73, 95% CI: [0.18; 1.29]), with a one unit increase in need associated with being over twice as likely to receive resources (OR=2.08). Note that in this model we still find an effect of sharing with less cooperative individuals (b=-0.01, 95% CI: [-0.002; -0.017]). This effect of need appears largely due to sharing with older individuals, as if the age component is removed from the composite need variable (keeping just number of dependent offspring and stored resources) then the effect of need on sharing, although still in the predicted direction, is much weaker (b=0.3, 95% CI: [-0.19; 0.79]). Compared to the model including need, we also find that that an

interaction term between need and kinship does not increase model fit (need model QIC=1089.6; interaction model QIC=1096.3), suggesting that this need-based sharing is directly towards kin and non-kin with equal frequency.

3.2. Reasons for Giving in the Sharing Game

We also asked why individuals gave to recipients, resulting in 1,001 answers. These were categorized according to various criteria relevant to the evolution of cooperation, such as kinship, reciprocity, need, and personal qualities, among others (figure 2 and table S4; for a similar procedure, see Gervais, 2017; Thomas et al., 2015). The most common reason for selecting an individual was genetic relatedness, accounting for over one-quarter of all nominations, while affinal relatedness accounted for one-sixth of all nominations. Collectively, over 40% of reasons given were based on kinship. The second largest category (~25% of nominations) was need-based sharing, including reasons such as old age, pregnancy, having many children, weakness, inability to work, having no food, or simply to help them. Around one in ten nominations referred to reciprocity between ego and alter. Personal qualities, such as kindness, leadership and generosity, although present, were less frequently mentioned (8.4%).

4. Discussion

These results demonstrate that experimental resource transfers among the Agta do not conform to predictions made by theories of cooperative assortativity. We fail to find evidence for both indirect reciprocity and cooperative homophily; individuals were neither more likely to select cooperative partners or those of a similar cooperative level. Rather, the Agta preferentially shared with less cooperative individuals, which may reflect need-based sharing. Accordingly, we also demonstrate

that individuals in need, particularly older Agta, were more likely to receive resources (although an independent effect of sharing with less cooperative individuals was still reported). This finding is bolstered by a qualitative analysis of the reasons individuals gave for sharing, with approximately one-quarter of all reasons coded as need- or helping-based (figure 2). Personal qualities, including kindness and generosity, alongside other competencies such as leadership and foraging skills, were mentioned three times less frequently than need-based reasons. The Agta may therefore use reputations for kindness or generosity to some extent when deciding to share with others, but sharing based on need appears to take precedence.

Since need-based sharing is a description of cooperation, not an adaptive explanation, understanding the evolutionary function of these patterns is essential. The lack of interaction between need and kinship suggests that resources in this game were given to needy camp-mates regardless of relatedness, meaning that indirect fitness benefits via kin selection cannot solely explain this need-based sharing. Comparable results were reported among Ache foragers where need, irrespective of relatedness, predicted real-world food-sharing (Allen-Arave et al., 2008). As there was no possibility of individuals taking resources from others, the current results also suggest that need-based sharing is not solely a consequence of tolerated theft (although other aspects of need-based transfers outside this experimental context may be explained by this). One potential functional explanation concerns reciprocity, but on a longer time-scale than assessed here (although an immediate effect of reciprocity was also observed). For instance, by helping those in need now, where the costs to the actor are low and the benefits to the recipient high, in the future where the roles may be reversed the former recipient may reciprocate (Trivers, 1971). This may be particularly important in hunter-gatherer contexts where

individual stochasticity in resource acquisition is high, combined with a life history where in families with many dependent offspring are frequently at a net deficit and in need of resources (Hill & Hurtado, 2009). The concept of resource value, rather than resource quantity, is pertinent here, as the same quantity of food has greater value for a needy, compared to a satiated, individual (Gurven, 2006). Taking this value asymmetry into consideration, rather than models where pay-offs are constant, greatly expands the potential for reciprocal cooperation to evolve (Doebeli & Knowlton, 1998). This implies that the quantities shared between individuals do not need to be identical, as long as the long-term resource values are equal (Gurven, 2006). For example, skilled hunters Ache who provisioned others received significantly more food while sick or injured relative to less-skilled hunters who provisioned others less often (Gurven, Allen-Arave, et al., 2000), while reciprocal non-kin sharing among vampire bats likely reflects similar evolutionary processes (Carter & Wilkinson, 2013). This long-term reciprocity based on asymmetrical pay-offs characterizes the need-based sharing observed among friends (Hruschka, 2010), thereby resolving the 'Banker's Paradox' (Tooby & Cosmides, 1996) and illustrating how non-kin cooperation – and friendship (Migliano et al., 2017) – can evolve.

Other functional reasons for this need-based sharing are also possible if benefits are not returned 'in-kind'. For instance, 'unconditional generosity' towards those in need may be a sexually selected strategy to exhibit one's phenotypic value by displaying qualities such as care, compassion and generosity to attract mates (Raihani & Smith, 2015). 'Charitable' donations may also enhance one's social standing, resulting in increased support in coalitions (Milinski, Semmann, & Krambeck, 2002; Patton, 2005) or cooperative hunting (Bliege Bird & Power, 2015).

While the benefits of being cooperative may not be apparent in the short-term 'in-kind' cooperative measure used here, a longer-term perspective investigating several different cooperative and fitness-relevant domains may highlight these benefits. Alternatively, other competencies such as foraging skill, leadership, storytelling prowess or knowledge may be more important in deciding with whom to interact and cooperate, rather than solely an individual's level of cooperativeness (Macfarlan & Lyle, 2015; Smith et al., 2017).

Although we find evidence for need-based sharing, an independent effect of sharing with less cooperative individuals was still reported. One possible reason for this is that our measure of need does not encompass all relevant components of need, such as being pregnant, nursing young infants (Hurtado, Hill, Hurtado, & Kaplan, 1992), or being ill/injured (Sugiyama & Chacon, 2000). Many of the stated reasons for sharing resources with those in need, including weakness and an inability to work, could not be explicitly included in our composite need variable due to a lack of quantitative data. Given the association between cooperativeness and other components of need (Smith et al., 2016), it is plausible that inclusion of these other factors may remove the residual effect of sharing with less cooperative individuals. Alternatively, perhaps there are reasons, other than need, why individuals would avoid sharing with cooperative individuals. For instance, foragers may shun highly-cooperative individuals to avoid being indebted to them (Woodburn, 1982), comparable to societies from Papua New Guinea rejecting over-generous offers in the Ultimatum Game (Henrich et al., 2005).

Our results suggest that mechanisms of cooperative assortativity may not have universal application as explanations for the evolution of human cooperation. There are several kinds of assortativity, however, not just by cooperativeness, which

prioritize specific partners over others. Cooperation in this experimental game is associated with assortativity by kinship and reciprocal partnerships, but in different contexts other assortative mechanisms may take precedence. For instance, in many large-scale societies kinship ties are weaker and interactions repeated less frequently, meaning that kin selection and reciprocal cooperation may be weaker forces in these contexts. Under these circumstances, mechanisms of cooperative assortment, such as indirect reciprocity, may become more important (as the proliferation of online seller rating systems attests; Livingston, 2005). As a concrete example of cross-cultural variation in cooperative strategies, both hunter-gatherer (Gurven, 2004) and pastoral (Aktipis et al., 2011) societies, which suffer repeatedly from resource shortfalls due to high levels of stochasticity in food production, appear to display need-based sharing as a risk-pooling strategy. In contrast, among the agricultural Mosuo in China needier households were not more likely to receive help (Thomas et al., 2018), potentially because the unpredictable variability in resource production required for reciprocal need-based cooperation to evolve is less pronounced in farming communities. Further cross-cultural research is required to explore how cooperative mechanisms vary with socioecological context.

These findings also have implications for models which use lab studies to investigate the evolution of cooperation. In many previous experimental studies supporting predictions made by theories of cooperative assortativity (Milinski, 2016; Milinski et al., 2002) the theory is examined in isolation. Yet, as demonstrated here, once other factors such as relatedness, reciprocity and need are taken into consideration in a real-world setting, individuals use these traits, rather than cues of cooperativeness, when deciding with whom to cooperate. Laboratory studies are useful proofs-of-concept, but real-world data are necessary to assess their predictive

power in ecologically valid contexts and to understand the social and ecological factors which influence cooperative behavior.

These findings suggest that need-based sharing, rather than cooperative assortativity, predicts patterns of experimental resource transfers among the Agta. However, these results possess several limitations. Firstly, we only explore one domain of cooperation (food-sharing). It is possible that cooperative assortativity may explain patterns of cooperation in other contexts, such as labor-sharing (Macfarlan et al., 2012), cooperative hunting (Bliege Bird & Power, 2015), child-care or selecting camp-mates (Apicella et al., 2012). Studies exploring multiple cooperative networks within a single society (see, for example, Jaeggi et al., 2016; Mace et al., 2018; Nolin, 2011) are required to explore this possibility. Nonetheless, the present results demonstrate that cooperative assortment is unlikely to influence 'in-kind' food-sharing decisions among the Agta.

Additionally, the present study does not aim to explore all facets of reputation-based cooperation. For instance, we do not assess whether individuals shared food in this game in order to gain a reputation for being cooperative, or how market effects of supply and demand influence cooperative decision-making (Barclay, 2013). Rather, we assume that individuals already possess a reputation for cooperativeness in real-world interactions and test whether these individuals are more likely to receive resources. This is a central prediction of all theories of cooperative assortativity. Further studies are required to explore how individuals earn a cooperative reputation and the additional nuances of cooperation in biological markets.

In addition to kin selection and immediate reciprocity, we therefore conclude that resource transfers among the Agta are largely based on need, rather than

mechanisms of cooperative assortment such as indirect reciprocity or cooperative homophily. This need-based sharing may represent delayed reciprocity or helping needy individuals for reputational benefits in other domains. This is likely due to a forager-specific ecology of high resource stochasticity resulting in repeated food shortfalls, necessitating need-based sharing as a system of long-term reciprocal exchange. These results therefore indicate that mechanisms of cooperative assortativity may not have universal application as explanations for the evolution of human cooperation, particularly prior to the advent of increasingly-anonymized interactions in large-scale societies.

Ethics

Ethical clearance was granted by the University Ethics Committee (Ethics code 3086/003). Fieldwork permission was granted by local government units, including the Mayors of the Municipalities visited and from the Department of Environmental and Natural Resources (DENR) as the research took place in a protected area.

Data Availability

The data and code associated with this research is available via figshare at 10.6084/m9.figshare.6960998 (this link will be made active upon publication).

Competing Interests

We have no competing interests.

Acknowledgements

We thank the Agta communities and research assistants for their help and hospitality in the field.

Funding

This work was supported by the Leverhulme Trust (grant no. RP2011 R045).

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Table 1: Comparison of the top models (within two QIC values of the best-fitting model) regarding who individuals gave resources to (*n*=272, dyads=1,312). Keeping age, sex and ego cooperativeness variables constant, 32 potential models were constructed and QIC values compared using all combinations of the variables: kinship, reciprocity, proximity, alter cooperativeness and cooperative homophily. ΔQIC denotes the difference in QIC values between models (with '0' being the top model), while model weight is a value between 0 and 1 which can be interpreted as the probability that a given model is the best fit to the data.

Model Variables	**QIC**	**ΔQIC**	**Model Weight (w_i)**
Kinship + Reciprocity + Alter Cooperativeness	1086.25	0	0.72
Kinship + Reciprocity + Alter Cooperativeness + Cooperative Homophily	1088.18	1.92	0.28

Figure 1: Forest plot displaying standardized log-odds estimates of giving resources to others, derived from the model averaging analysis (table S2; *n*=272, dyads=1,312; see table 1 for component models). Note that not all variables are displayed. Abbreviations: PK=Primary kin; DK=Distant kin; NR=Non-relatives. Error bars denote 95% confidence intervals.

Figure 2: Pie chart displaying the proportion of reasons, split by category, for giving to others (total reasons=1,001: for additional details see table S4).

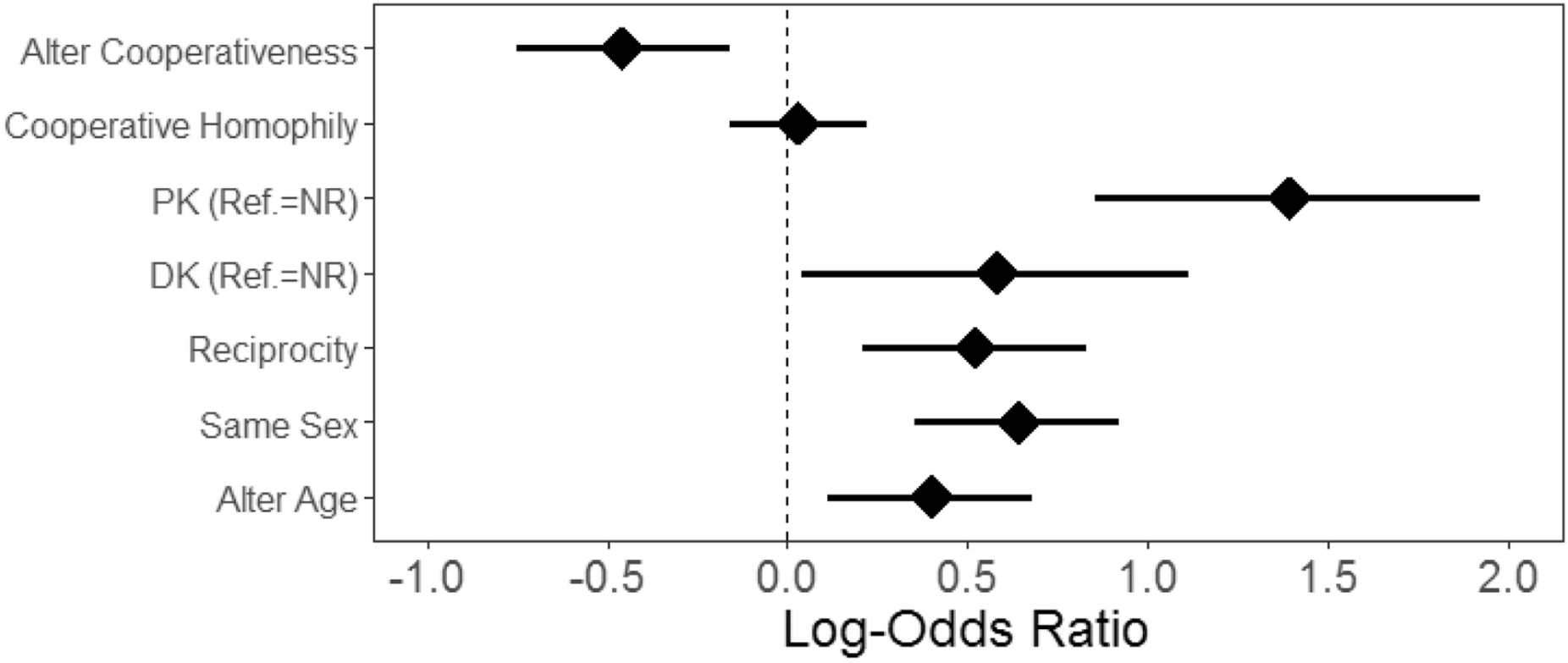
Alter Cooperativeness
Cooperative Homophily
PK (Ref.=NR)
DK (Ref.=NR)
Reciprocity
Same Sex
Alter Age
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Log-Odds Ratio

Figure 1

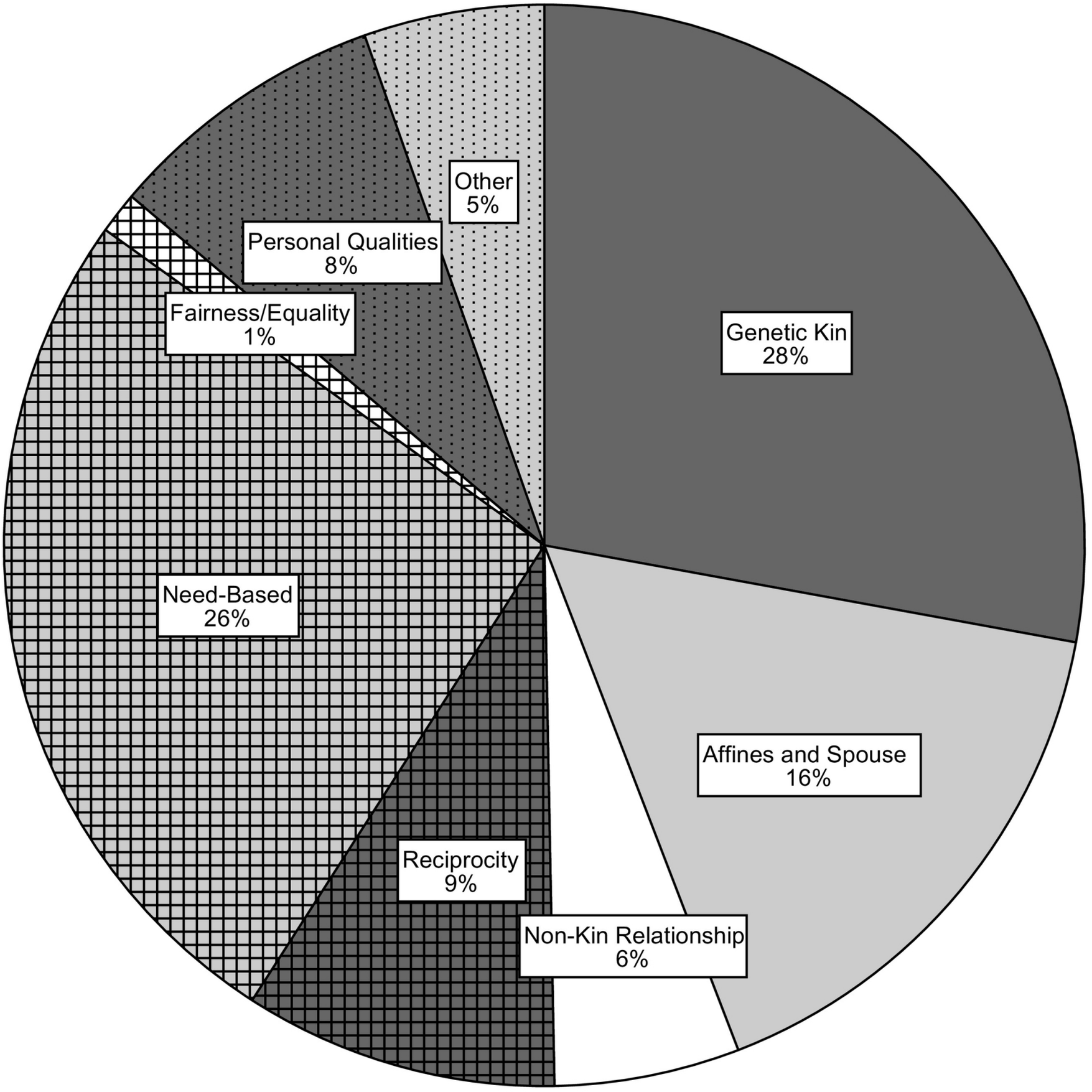
Other
5%
Personal Qualities
8%
Fairness/Equality
1%
Genetic Kin
28%
Need-Based
26%
Affines and Spouse
16%
Reciprocity
9%
Non-Kin Relationship
6%

Figure 2